



A Bimodal Feeding System in a Stream-Dwelling Larva of *Rhacophorus* from Borneo

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Source: *Copeia*, Aug. 18, 1992, Vol. 1992, No. 3 (Aug. 18, 1992), pp. 887-890

Published by: American Society of Ichthyologists and Herpetologists (ASIH)

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SHORTER CONTRIBUTIONS: HERPETOLOGY

Copeia, 1992(3), p. 887
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THE RELATIONSHIP OF BATRACHOLOGY TO HERPETOLOGY—Amphibians and reptiles have been recognized as distinct classes of vertebrates since the first half of the last century. Nevertheless, their study usually has been referred to the same subdiscipline of zoology, namely herpetology. The past decade has seen the resurgence of the term “batrachology”—used already by Steindachner (1864)—for the study of amphibians (more precisely, the Batrachia or Lissamphibia).

Dubois (1991) reviewed the case for propagating batrachology as a distinct scientific discipline and some pertinent terminological problems. Specialization in systematic groups should facilitate integration of studies in various fields of research. Dubois (1991) argued that associating amphibians with reptiles in herpetology impeded such synthesis in amphibian biology. In particular, developmental biology of amphibians is almost absent from herpetological meetings and journals. Recognition of batrachology as a discrete discipline aims at improving communication among scientists and thus increasing efficiency of research and conservation of amphibians. To promote this recognition of batrachology, Dubois (1991) suggested using the term herpetology in a restrictive sense, referring only to the study of reptiles.

Although I concur with Dubois' (1991) desire to give amphibians and their scientific study overdue recognition, I disagree with this proposal for two reasons. Even though a few prominent nineteenth-century authors used the term herpetology in the sense now advocated by Dubois (1991), all societies and journals bearing herpetology in their names understand this as the “study of amphibians and reptiles.” If a number of zoologists started using the term herpetology in a restrictive sense, meaning “study of reptiles” or perhaps “study of snakes,” this would generate confusion rather than clarity. Second, the class Reptilia—comprising all amniotes except mammals and birds—has become a paradigm of a paraphyletic group that, according to the opinion of many systematists, should not have a place in the natural system at all (e.g., Wiley, 1981; Ax, 1988). Thus, “reptiles” (the word, not the beasts) may become

obsolete soon and it would make little sense to designate any term for their study.

To support batrachology as a distinct scientific discipline necessitates neither a change in the meaning of herpetology nor the use of a new term for the study of reptiles. We can as well acknowledge that herpetology, like ichthyology, is a collective discipline, dealing with a grade, but not with a class, of vertebrates. The use of these terms is justified by the historical development of biology rather than by our current understanding of systematics; certainly they can coexist with other terms relating to monophyletic groups. The reasons for establishing batrachology as a discipline in its own right are good (Dubois, 1991). As for reptiles, it depends upon the students of the major reptilian taxa to determine whether they will find it worthwhile to redefine their special disciplines as “cheloniology,” “ophidiology,” etc.

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Copeia, 1992(3), pp. 887–890
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A BIMODAL FEEDING SYSTEM IN A STREAM-DWELLING LARVA OF *RHACOPHORUS* FROM BORNEO.—In the last three years, there have been reports of successful development of tadpoles in the absence of feeding in genera in which the norm is active ingestion of food throughout the larval period.

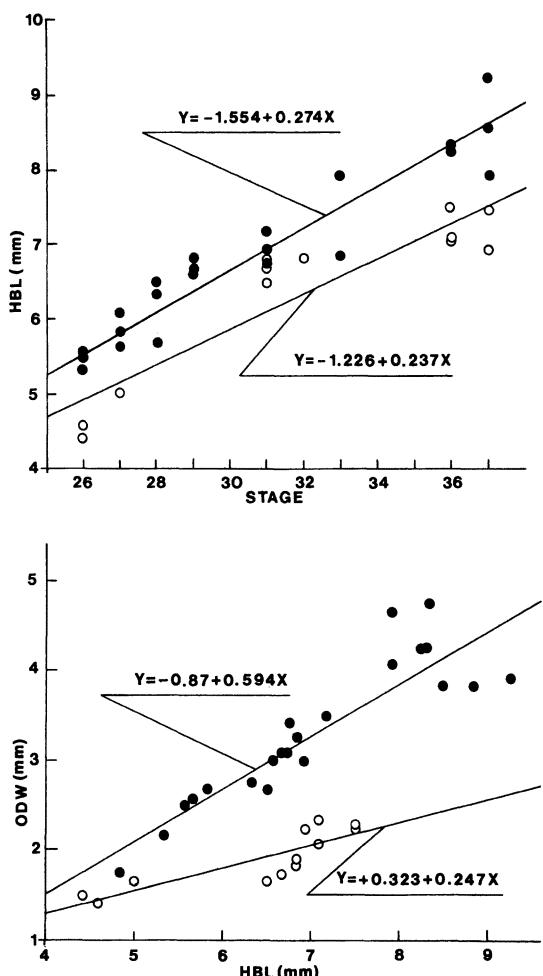


Fig. 1. Developmental relations of exotrophic (solid circles and solid lines) and endotrophic (open circles and dashed lines) forms of larval *Rhacophorus gauni* (Inger). Top, relation of head-body length (HBL) to stage (Gosner, 1960). Bottom, relation of oral disc width (ODW) to HBL.

Larval *Bufo periglenes* apparently can complete development as either endotrophs or exotrophs (Crump, 1989) and apparently larval *B. hae-matiticus* can also (McDiarmid and Altig, 1990). Both species are additionally remarkable among species of *Bufo* in having relatively small clutches of large ova, clearly essential for this habit. Two Japanese frogs, *Rana tagoi* and *R. sakuraii*, have small clutches of very large ova and complete larval development without feeding (Kusano and Fukuyama, 1989; Maeda and Matsui, 1989). I report here on a larval rhacophorid

anuran that has both exotrophic and endotrophic habits. This constitutes the first known instance of an endotrophic stream-dwelling rhacophorid larva in Southeast Asia.

Larval *Rhacophorus gauni* (Inger) live in riffles and, less often, in torrents of small streams flowing through rain forests in Borneo (Inger and Tan, 1990). Tadpoles have been found at nine localities from central Sarawak to eastern Sabah, a distance of 650 km. Distinguishing features of these tadpoles include an expanded, cuplike oral disc; labial tooth formula 4(3–4)/3(1); and heavy, coarsely serrated jaw sheaths. At one of the localities, Danum Valley Field Centre, eastern Sabah ($5^{\circ}06'N/118^{\circ}12'E$), two morphotypes have been taken from the same collecting stations on three streams over a four-year period. Most of these tadpoles have the gut coiled in a manner typical of feeding tadpoles, with 6–9 coils by stage 26 (Gosner, 1960) and 7–11 coils in stages 27–37. The gut is filled with fine particles, again, typical of feeding tadpoles. Twelve tadpoles, stages 26–37, have a yolk-filled gut with few or no coils. In these 12, the oral disc, though still cuplike, is smaller relative to the body and the labial teeth and jaw sheaths are correspondingly reduced.

Methods:—Staging follows the system of Gosner (1960); and labial tooth nomenclature and formulas follow the system of Altig (1970). Terminology of structures of the oral disc follow suggestions of Altig and McDiarmid (McDiarmid, pers. comm.). Measurements were made with an ocular grid at $12\times$. Gut coils were counted in a rostrocaudal plane following the method of Nodzenski et al. (1989). All tadpoles were fixed and maintained in buffered formalin. All adult and larval specimens of *R. gauni* studied are in the collections of the Field Museum of Natural History (FMNH). Tadpoles examined, in addition to those listed in Inger and Tan (1990), are FMNH 241921–31 (Danum Valley, Sabah) and 244173–77 (Mendolong, Sabah).

Results and discussion:—Comparisons are limited to the co-occurring samples from Danum. The two forms differ slightly in head-body lengths (HBL) at corresponding stages, but the regressions of HBL on stage are not significantly different (Fig. 1). However, differences in oral disc width (ODW) are significant. The ratio ODW/HBL in stages 27–37 in the non-feeding form is 0.26–0.34 ($n = 12$) and in the

feeding morph is 0.41–0.59 ($n = 26$). The slopes of regressions of ODW on HBL (Fig. 1) are significantly different ($P < 0.01$).

Other features of the oral disc also differ. The labial teeth and jaw sheaths of the endotrophic larvae are smaller than those of the feeding ones. These differences are reflected in, but not completely defined by, differences in numbers of labial teeth and serrae on the jaw sheaths. Labial teeth in the right half of A3 are 18–28 (mean \pm SD = 21.7 ± 3.20 , $n = 10$) in the nonfeeding form and 28–38 (33.5 ± 3.70 , $n = 11$) in the feeding form; serrae in the upper jaw sheath are 6–13 (9.1 ± 1.91 , $n = 10$) and 14–20 (16.3 ± 2.05 , $n = 11$), respectively. In a few tadpoles of the endotrophic morph, the jaw sheaths are not complete medially. In the characters just discussed, all *R. gauni* tadpoles from other localities agree with the exotrophic form at Danum.

Two issues must be resolved. First, do the two morphotypes represent separate species? The known Bornean stream-dwelling tadpoles of the genus *Rhacophorus* are sharply distinct from one another (Inger, 1985; Inger and Tan, 1990). Interspecific variation includes serration and relative sizes of jaw sheaths, number of rows of labial teeth, distribution of labial papillae, and pigmentation. In all of these respects, the two forms of larval *gauni* are identical, except for the overall reduction of the oral disc and its parts. The morphological differences between the forms are all related to the differences in feeding and could have been effected by a simple genetic change.

Even if the two forms lack interspecific differences of the sort usually observed in Bornean riparian *Rhacophorus*, they may nonetheless be larvae of separate species. The second issue, then, concerns the number of potential parental species at Danum Valley. Adults of *Rhacophorus gauni* were observed in each of four periods of study at Danum Valley (1986, 1987, 1989, 1990). The 67 adults collected show little variation. Three lack the palpebral "horn" characteristic of the species, and one lacks the enamellike, white, suborbital spot. These variants appear elsewhere in the species range: for example, two of 10 from Mendolong, Sabah, 275 km west of Danum Valley, lack the suborbital spot. Populations at four sites in the Crocker Range, Sabah (50–150 km north of Mendolong), lack the palpebral "horn."

The evidence permits just two alternative

conclusions: (1) only a single species of adults for these tadpoles exists at Danum Valley, or (2) a second species exists that has not yet been discovered. Repeated observation over four field seasons of a single species along the streams where both larval types were found makes the second alternative very unlikely. The following discussion assumes that only a single species, *Rhacophorus gauni*, is involved.

Because the developmental series of the yolk-laden form ends at stage 37, it was not possible to demonstrate conclusively that these tadpoles reach metamorphosis without feeding. However, the large amount of yolk still remaining in the gut of stage 37 individuals suggests they might succeed in completing development. Another open question concerns genetic relations of the two feeding types: Are they produced in separate clutches, or does a single clutch of eggs yield both forms? The only clutch of ovulated ova available shows a limited, continuous size range of 2.33–2.75 mm.

Both of the facultatively endotrophic bufonid tadpoles live in small pools (Crump, 1989; McDiarmid and Altig, 1990), and Crump suggested that this habit increases the likelihood for survival to metamorphosis in an environment of uncertain duration and limited food supply. The Bornean rhacophorid tadpoles, however, live in permanent streams. Although no measure of food abundance is available, tadpoles of at least seven genera and 10 species are known to complete development in these waters at the same time and some in the same microhabitats (unpubl. data). The endotrophic Japanese ranid tadpoles also live in permanent streams. Crump (1989) determined that unfed tadpoles of *B. periglenes* metamorphose in less time than fed ones. Possibly the nonfeeding larval *R. gauni* also complete development in less time than the exotrophic ones. Even if that is true, the ecological advantage of a shorter aquatic stage in this environment is far from clear.

Acknowledgments.—I am grateful to the authorities of Sabah Parks, Sabah Forest Industries, and Yayasan Sabah for permission to work in areas under their control. I also thank the following people for their help in the field: S. B. Emerson, F. L. Inger, J. Murphy, R. B. Stuebing, H. K. Voris, and P. Yambun. Field work was partially supported by the Marshall Field

III Fund of the Field Museum and the National Geographic Society.

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Copeia, 1992(3), pp. 890–894
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THE BASIC MECHANICS OF ASCENT AND DESCENT BY ANURAN LARVAE (*XENOPUS LAEVIS*).—The kinematics of locomotion for amphibian larvae has received much attention in recent studies using high speed cinematography (e.g., Wassersug and Hoff, 1985; Hoff and Wassersug, 1986; Hoff et al., 1990). However, in all these investigations, data were collected by filming solely from above, so only movement in the horizontal plane was exam-

ined. Despite all these studies, one question remains unaddressed: How do tadpoles dive or ascend?

Most fishes have mobile pectoral and pelvic fins which they use to effect turns in the vertical plane. By changing the angle of attach for those lateral appendages, a swimming fish generates torque through its transverse axis causing its head to pitch up or down. But tadpoles, at least until near metamorphosis, lack mobile lateral appendages; yet they ascend and descend perfectly well. To the best of my knowledge the question of how tadpoles effect turns in the vertical plane has not been explored in the kinematic literature.

There are fundamentally three ways that a nektonic organism lacking lateral appendages could dive. One way would be to change buoyancy by, for example, compressing air in a gas bladder. This mechanism might apply to some tadpoles—those with inflated lungs—but certainly not to all. Many tadpoles, such as those in the species-rich genus *Bufo* (toads), do not inflate their lungs until metamorphosis. Nevertheless they are perfectly capable of rapid ascent and descent in the water column.

The second, and most obvious mechanism, is to flex the axial skeleton. By simply pitching the snout up or down relative to the tail, an aquatic organism could redirect itself in the vertical plane. It has been claimed that the tadpole "is able to initiate upward and downward movements by flexing the tail upward and downward" (Affleck, 1950: 359). Whereas Affleck believed the tadpole tail was flexible in the vertical plane, he provided no supporting evidence. Based on anecdotal field observations and gross myology, pure axial flexion in the head/body has been inferred to occur in the bizarre, shovel-snouted tadpole of *Otophryne robusta* during burrowing (Wassersug and Pyburn, 1987). Otherwise, I know of no documentation for the contention that typical pond larvae are capable of significant bending in the sagittal plane at the base of the tail or anywhere else along the body axis.

There are a variety of reasons why flexion and extension of the body axis in the sagittal plane might be limited in tadpoles compared to, for instance, salamander larvae. The short, common head/body of pond tadpoles is generally globose and seemingly inflexible. Tadpoles, along with adult frogs, have the shortest vertebral column of any organism. They lack a defined cervical region that might allow for ex-